

History of the Pliocene Molluscan Fauna of Northern Japan

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(1 Text figure)

INTRODUCTION

AS A STEP IN UNDERSTANDING the origin of the modern North Pacific molluscan fauna, a study of the Pliocene molluscan fauna of northern Japan was undertaken. The principal aim of the study was to interpret the probable areas of origin and the dispersal history of bivalve and gastropod genera and subgenera which make up that fauna. Brief comments concerning development of the Japanese Cenozoic molluscan fauna and a comparison of Tethyan immigrant history in Japan and New Zealand are included.

The findings in this study are based on 126 taxa including 107 genera and 19 subgenera. Taxonomic designations and age assignments by previous workers were generally followed because a comprehensive re-evaluation of the literature was not possible within the scope of the study. Because there are gaps in the knowledge of some genera, the findings presented herein range from plausible to speculative. The place of earliest occurrence of fossil taxa and their chronologic and geographic distributions served as the principal bases for interpreting the place of origin and migratory history of mollusks.

Over 200 reports concerning the Mesozoic and Cenozoic molluscan records of the Pacific basin, and to a lesser extent those of the western Tethys and New World, were examined. Only those papers essential to the preparation of this report have been cited. The major works on Jurassic and Cretaceous bivalves by HAYAMI (1961, 1965 and 1966) and the Paleogene molluscan record by OYAMA, MIZUNO & SAKAMOTO (1960) were especially useful for the pre-Neogene molluscan record in Japan. Sources which were important in gleaning the Neogene molluscan record of Japan include check lists of Japanese Cenozoic marine mollusca by HATAI & NISIYAMA (1952) and MASUDA & NODA (1976); additional pertinent references are to be found in the bibliographies of these works. The Treatise of Inverte-

brate Paleontology (Part N. vols. 1, 2 and 3; MOORE, R.C., 1969) served as a basic source for systematic biogeographic and chronologic information for bivalves; WENZ (1938-44) and KEEN (1963) served in a similar way for gastropods.

The results of this study, in summary form, show only general trends concerning the provenance of Pliocene bivalve and gastropod genera of northern Japan. It is hoped that the study will be stimulating and form a useful basis for more refined studies of this fascinating subject.

THE PLIOCENE FAUNA

The Pliocene fauna of this study is an artificial aggregate of molluscan assemblages from major Pliocene deposits of northernmost Honshu and Hokkaido. The Honshu assemblages were described from stratigraphic units exposed in Aomori Prefecture at the extreme north end of Honshu Island. These deposits and the citations followed in this study include: (1) Sannohe Group (CHINZEI 1959, 1961) and (2) Narusewa, Higashimeya, Totezawa, and Dai-shaka formations of the Tsugaru sequence (Iwai, 1965). The Hokkaido assemblages were described from the Setana Formation (Uozumi, 1962; Kanno, 1962) and the Takikawa Formation (Uozumi, 1962). The fauna of the Hamada Formation (Hatai, Masuda & Suzuki, 1961) of Aomori Prefecture was not considered in this paper but the majority of its bivalve and gastropod genera is represented in the fauna herein delineated. The Pliocene fauna reflects a variety of marine environments ranging from shallow to deep water facies and represents molluscan life in 4 or 5 marine basins. On the whole, the generic and subgeneric composition of the fauna is similar to that of the northern temperate/boreal regions of the North Pacific, with some elements more characteristic of lower latitudes present. No attempt was made to subdivide the fauna in a time-stratigraphic sense.

MESOZOIC ROOTS

A number of genera and subgenera found in the Pliocene fauna of northern Japan were residents of Japanese waters as early as Jurassic and Cretaceous times (22; 17%). The following genera are present in the Jurassic record: *Nuculana*, *Solemya*, *Modiolus*, *Lima*, *Limatula*, *Astarte*, *Ostrea*, *Cuspidaria*, *Pholadomya*, *Thracia*, and *Mytilus*. Genera which evidently made first appearances in Japanese seas during Cretaceous times include: *Acila* (*Truncacila*), *Yoldia*, *Glycymeris*, *Chlamys*, *Barbatia*, *Nemocardium*, *Panope*, *Tellina*, *Spondylus*, *Turritella*, and *Cerithium*. Other genera have been reported from the Cretaceous of Japan but their generic assignments are considered doubtful. These "Cretaceous" genera and their probable earliest valid occurrences in Japan are: (1) EOCENE - *Siliqua*, *Anomia*, and *Callista*; (2) OLIGOCENE - *Portlandia*, *Arca*, *Monia*, *Lucinoma*, *Laevicardium*, *Spisula*, and *Epitonium*; (3) MIOCENE - *Chama* and *Natica*.

Of the Jurassic and Cretaceous taxa herein considered to be valid residents of Japan during the Mesozoic, a few have histories extending much farther back in time in other parts of the world including *Solemya* (Devonian), *Modiolus* (Devonian), and *Pholadomya* (Triassic). The first Japanese occurrences of the balance of the Mesozoic genera and subgenera, however, very closely approximate their earliest known occurrences elsewhere in the world. Virtually all of the Mesozoic genera and subgenera have rather cosmopolitan fossil records so that, at present, there is no strong basis for identifying a relatively specific geographic place of origin for any of them. Many of these genera have substantial distributions in the Tethyan region. Judging from their extensive Cenozoic fossil records in Japan, these taxa have evidently persisted in Japanese waters from Mesozoic time up to the present. It is possible that other populations, representing the same genera that lived in Cretaceous and Jurassic seas of Japan, may have been reintroduced to Japan through migration during the Cenozoic. The apparent lack of a fossil record between Cretaceous and early Miocene time suggests that *Limatula* and *Spondylus* may represent two such populations.

CENOZOIC HISTORY

The overwhelming majority of genera and subgenera (109; 84%) making up the Pliocene fauna of northern Japan were introduced into Japanese seas during the Cenozoic Era. Source areas include the North Pacific (42%), Tethyan region (40%) and possibly the Atlantic basin (1%).

NORTH PACIFIC INFLUENCE

North Pacific genera and subgenera include: (1) those that evolved in Japanese waters or close to them, (2) those that evolved in the eastern North Pacific and migrated to Japan, and (3) those that evolved in the North Pacific realm but whose specific place of origin is not clear.

Genera and subgenera believed to have originated in Japanese waters, or close by, and their probable times of origin are: Eocene - *Neptunea*; Oligocene - *Mya*; Miocene - *Mizuhopecten*, *Fortipecten*, *Swiftopecten*, *Kotorapecten*, *Placopecten*, *Coraeophos*, *Protothaca* (*Callichaca*); Pliocene - *Yabepecten*, *Turritella* (*Neohaustator*), *T.* (*Hataiella*) and *Dosinia* (*Kaneharaiia*).

The fossil record of at least 4 genera seems to favor an origin somewhere in the northeastern Pacific region followed by westward migration to Japan; these genera and subgenera, and their earliest definite occurrences in Japan, are: Oligocene - *Fulgoraria*; Miocene - *Trichotropis*, *Fusitriton*; Pliocene - "Macron." All of these genera occur earlier in the eastern Pacific by, at least, one full epoch.

The area of origin of the balance of North Pacific genera and subgenera cannot be determined at this time. These taxa and their earliest occurrences in Japan are: Eocene - *Cyclina*, *Macoma*; Oligocene - *Acila* (*Acila*), *Thyasira* (*Conchocele*), *Clinocardium*, *Serripes*, *Spisula* (*Macromeris*), *Tellina* (*Peronidea*), *Epitonium* (*Boreoscala*), *Crepidula*, *Beringius*, *Buccinum*; Miocene - *Saxidomus*, *Tresus*, *Musculus*, *Panomya*, "Pandora", *Pholadidea*, *Puncturella*, *Menestho*, *Leucosyrinx*, *Lora*, *Natica* (*Cryptonatica*), *Trophonopsis*, *Nucella*, *Limopsis* (*Empleconia*); Pliocene - *Spisula* (*Pseudocardium*), *Fabulina*, *Ophioidermella*, *Liloa*, *Crepipatella*, *Mohnia*, *Colus*, *Suavodrilina*, *Antiplanes* (*Rectiplanes*) and *Propebela*.

TETHYAN INFLUENCE

The eastern Tethyan region furnished the following genera and subgenera at various times during the Cenozoic Era: Eocene - *Crenella*, *Mactra*, *Anomia*, *Siliqua*, *Callista*, *Lima* (*Acesta*), *Polinices*; Oligocene - *Spisula*, *Monia*, *Arca*, *Anadara*, *Septifer*, *Lucinoma*, *Venericardia* (*Cyclocardia*), *Laevicardium*, *L.* (*Fulvia*), *Dosinia*, *Meretrix*, *Clementia*, *Solen*, *Portlandia*, *Calliostoma*, *Nassarius*, *Epitonium*, *Hiatella*; Miocene - *Spondylus*, *Limatula*, *Pillucina*, *Chama*, *Venerupis*, *Pseudogrammatodon*, *Lithophaga*, *Mitrella*, *Olivella*, *Inquisitor*, *Bittium*, *Batillaria*, *Sinum*, *Cancellaria*, *Cocculina*, *Turcica*; Pliocene - *Nucinella* (*Huxleyia*), *Leptaxinus*, *Mysella*, *Gari*, *Dosina*

(*Phacosoma*), *Umbonium*, *Leptothyra*, *Serpulorbis*, *Alvania*, and *Fusinus*. The appearance of *Crenella* in the Eocene followed by a gap in the record until middle Miocene suggests that *Crenella* may have migrated to Japan on more than one occasion as has been suggested earlier in this paper for *Limatula* and *Spondylus*.

ATLANTIC INFLUENCE

The genus *Mercenaria* is represented in Japan by at least 4 species with an early Miocene to Recent time span. One species has also been reported in the northeastern Pacific but its occurrence there is regarded as of possible accidental origin (GRANT & GALE, 1931). In the northwestern Atlantic province, *Mercenaria* has a well-established history from Oligocene to Recent within a geographic span ranging from Nova Scotia to the Gulf of Mexico (PALMER, 1927). The earlier occurrence and development in the New World suggests that *Mercenaria* may have originated in the Gulf Coast area (Oligocene occurrences) and migrated to Japan via the Bering Sea in latest Oligocene/early Miocene time. If *Mercenaria* used the Bering Sea, then it would appear this dispersal route was open in late Oligocene-early Miocene time, which is earlier than the earliest Cenozoic (late Miocene) opening proposed by DURHAM & MACNEIL (1967). Other possible explanations for the apparent presence of *Mercenaria* in the western Pacific and Atlantic are: (1) polyphyletic origin, (2) migration into the western Pacific via Central America and the eastern Pacific, and (3) misidentification of fossils (not likely).

DISCUSSION AND SPECULATION

The above findings indicate that the generic and subgeneric composition of the fauna of northern Japan developed over a Jurassic-Pliocene time span from three main sources: (1) cosmopolitan Mesozoic holdovers of uncertain geographic provenance (17%), (2) North Pacific Cenozoic elements (42%), and (3) Tethyan immigrants of Cenozoic age (40%). A possible single Atlantic immigrant forms an additional Cenozoic source (1%). The Tethyan, North Pacific and Mesozoic elements are commonly associated at individual Pliocene fossil localities; no localities have been recognized in this study which are composed of genera and subgenera from a single source.

In terms of percentage of the total northern Pliocene fauna, the Tethyan (T) generic and subgeneric contribution appears to predominate over the North Pacific (NP) element during the Eocene (T-5%; NP-3%) and Oligo-

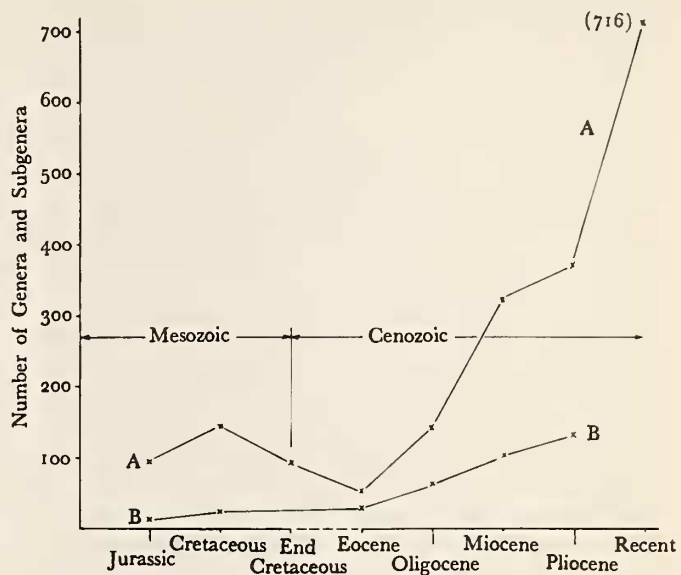


Figure 1

Comparison between (A) Diversity of total Japanese marine bivalve/gastropod fauna and (B) cumulative appearance of the northern Pliocene marine bivalve/gastropod fauna (The Paleocene is not generally recognized in Japan)

cene (T-15%; NP-10%); the North Pacific additions predominate in the Miocene (T-11%; NP-18%) and in the Pliocene (T-8%; NP-14%). The predominance of North Pacific elements in the Miocene and Pliocene may or may not be significant considering the size of the Pliocene fauna, but the figures are somewhat consistent with the consequences of the well-established southward shift of isotherms in the northeastern Pacific during the Cenozoic (DURHAM, 1950).

The appearance of genera and subgenera of the Pliocene fauna of northern Japan, as well as the generic diversity of the Japanese molluscan fauna (bivalves and gastropods combined), during the Mesozoic and Cenozoic Eras, is shown in Figure 1. The appearance of Pliocene genera mirrors the generic diversity of the total Japanese fauna, especially in terms of the fairly rapid and consistent increase during the Cenozoic. The total Japanese faunal diversity curve, however, reveals two features which are not reflected in the Pliocene curve.

The first of these is the sharp decline in the number of genera during the latest Mesozoic/earliest Cenozoic interval. This depletion of genera is probably a reflection of mass extinctions which took place on a world-wide scale at

the close of the Cretaceous. The second feature is the abrupt increase in numbers of genera/subgenera during the Oligocene/Miocene interval. This rapid increase may be the result of a combination of events related to the opening of the Sea of Japan and establishment of Japan as an island complex.

Japan, as now viewed within the context of plate tectonic theory, is thought to have been originally a coastal strip attached to the Asian continent just north of Korea (UYEDA & MIYASHIRO, 1974). Later, under the influence of tensional forces and sea-floor spreading, Japan was detached from the continent and carried eastward (300-800 km) with the Sea of Japan forming behind it. The rifting history is not well understood. UYEDA & MIYASHIRO (1974) consider rifting to have begun in Late Cretaceous/early Tertiary time; Dickinson (personal commun., 1977) believes that the Sea of Japan began to open sometime in post-Cretaceous time. HILDE & WAGEMAN (1973) have interpreted two spreading centers in the Sea of Japan of Late Cretaceous/early Tertiary and Miocene age; high heat flow in the Sea of Japan suggests that sea floor spreading may still be underway.

The early Tertiary fossil record in Japan suggests that from Eocene through Oligocene time, the Japanese region was progressively cooling from tropical to temperate conditions, a trend possibly related to the southern shift of isotherms interpreted by DURHAM (1950) for the north-eastern Pacific. Later, perhaps during latest Oligocene time, Japan was detached from the Asian coast and carried southeasterly directly into the path of the northeasterly flowing paleo-Kuroshio current which, presumably drew from warm equatorial waters of the southwest Pacific. Such a circumstance might then result in a change to subtropical and tropical conditions which indeed appear to characterize the middle Miocene of Japan (MINATO, GORAI & HUNASHI, 1965). Thus a part of the abrupt rise in molluscan genera during Oligocene/Miocene time may be attributable to rapid colonization by Tethyan immigrants following "intersection" of Japan and the warm, paleo-Kuroshio current, which would doubtless be carrying a stream of molluscan larva from the Tethyan region.

A second factor which may help explain the abrupt increase of genera during the Oligocene/Miocene interval, is the vast change in environmental conditions caused by changing from an unprotected, open coastal setting (before rifting) to that of a protected inland sea, flanked by a 2000 km-long archipelago (Japan) fronting on the open Pacific (after rifting). A vast new complex of shallow marine environments was almost surely created which in turn would act to heighten the potential for developing new genera through evolutionary processes as well as to provide a new

array of shallow water habitats not formerly available to existing genera and subgenera. The opening of new environments would be expected to increase the diversity of forms living in the region.

The roles of paleogeography, crustal movements, and current systems may help explain the Cenozoic molluscan history of New Zealand which is located in approximately the same latitudinal span in the southern hemisphere as Japan is in the northern hemisphere. FLEMING (1967) has shown that New Zealand, like Japan, received a strong influx of Tethyan bivalves and gastropods (about 169 genera) during the Cenozoic Era. Of special interest is the relatively high rate of extinction of Tethyan genera in New Zealand. According to FLEMING (*op. cit.*) about 65% (109) of all Tethyan immigrants reaching New Zealand during the Cenozoic became extinct before the end of that era, many dying out soon after their arrival in New Zealand. Extinction was not concentrated during a few critical periods, but was rather well-distributed during the entire Cenozoic. By contrast, the data available to the writer, through literature and discussion with colleagues, indicate that perhaps no more than seven genera and subgenera out of not less than 300 Tethyan immigrants, became extinct in the Cenozoic of Japan. These taxa and their times of extinction are: EOCENE - *Crassatellites* (*Eucrassatella*), *Venericardia* (*Venericor*), *Lima* (*Meotolima*); Oligocene - *Venericardia* (*Venericardia*), *Claibornites*, *Hubertschenkia*; Miocene - *Vicarya*. This apparently marked difference in extinction histories would seem to indicate that the Tethyan immigrants of New Zealand were subject to rather high levels of adaptive stress throughout the Cenozoic whereas in Japan conditions seem to have been equable for all elements present (Tethyan, North Pacific, and Mesozoic holdovers) and well within the adaptive capability of the bivalve and gastropod genera there.

A number of factors suggest that New Zealand was indeed subjected to significantly changing environments during the full span of the Cenozoic (KENNETT, HOUTZ, ANDREWS *et al.*, 1974). These include (1) the persistent northward drift of New Zealand of some 1000-1300 km between the Eocene and Recent. [During the same interval, Japan apparently remained at essentially the same latitudinal position (DIETZ & HOLDEN, 1970)] (2) Exposure of New Zealand to the cold circum-Antarctic current beginning in the Oligocene, caused by a progressively enlarging strait between a northward-drifting Australia and Antarctica, and (3) progressive alteration and interference of southeast-flowing Indo-Pacific equatorial currents carrying Tethyan molluscan larva to New Zealand by the northward-drifting Australia. Antarctic glacial episodes in the Eocene, Oligocene, late Miocene, Pliocene, and Pleis-

tocene (KENNETT, BURNS, ANDREWS *et al.*, 1972; SHACKLETON & KENNETT, 1975) also would be expected to have persistently affected the marine conditions in New Zealand. The New Zealand and Japanese histories sketched above, though reflecting some differences in detail, would seem to point up the growing importance of the effects of plate movements, paleo-current circulations and paleogeographic settings, in addition to more local events, in interpreting the biogeographic history of marine organisms.

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